SYSTEMATIC AND ECOLOGIC SIGNIFICANCE OF FOSSIL HARDWOODS. EXAMPLES FROM BIG BEND NATIONAL PARK, YELLOWSTONE NATIONAL PARK, AND FLORISSANT NATIONAL MONUMENT

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INTRODUCTION

Spectacular and abundant remains of petrified woods occur at Big Bend National Park, Texas, Yellowstone National Park, Wyoming, and Florissant Fossil Beds National Monument, Colorado, of Cretaceous and Paleocene, Middle Eocene, and late Eocene ages, respectively. These woods provide valuable data about the past distribution and diversity of flowering plants and changes in climate and vegetation through geologic time. Woody remains provide direct evidence of whether a fossil plant was a tree, shrub, or woody vine, and so are useful for interpreting vegetation type. Growth ring characteristics and the sizes and

distributions of the water conducting element in fossil woods provide information valuable for interpreting past climates and climate change.

Usually the first questions asked about petrified wood are- What is it? What is its name? Visitors who see petrified wood ask these questions out of general curiosity, but these are questions that need answering before a wood can provide data useful for understanding the past distribution and diversity of woody plants. However, answering 'what is it?' often is not easy, particularly for hard wood from the Cretaceous and early Tertiary. Identifying a fossil wood generally requires preparation of thin sections of three different views of that wood and use of a microscope. Considerable comparative work is necessary to establish whether the wood is similar to or different from wood of present-day plants.

Today there are tens of thousand of tree species, and so determining the relationship of a fossil wood to

Recent plants often is quite time-consuming. Most present-day trees fall into two groups: softwoods (the conifers which produce their seeds in cones, for example, pine, spruce, redwood) and hardwoods (dicotyledonous angiosperms which produce seed in flowers,for example, oak, maple, elm). these two groups have distinct wood structure. this paper only discusses only fossil hardwoods, in other words, woody dicotyledons, a group that is of more recent origin (Cretaceous) than the softwoods.

Generally, the older a wood is, the less likely it is that there is an extant wood with the same combination of characters as the fossil. In the eocene forests of North America, eastern Asia, southeast Asia, Central and South America, or even Africa (e.g. the Clarno flora of eastern Oregon, in the John Day Fossil Beds National Monument, Manchester in press), this means that comparative work cannot be restricted to trees that grow in the geographic region at present. Databases with information on the anatomy of extant fossil woods help with this comparative work (Wheeler et al. 1986; LaPasha and Wheeler and Baas, 1991).

Following are brief summaries of some work done on fossil wood from Big Bend, Yellowstone, and Florissant. These summaries are intended to indicate the importance of the fossil woods from these localities for helping answer questions about the history of woody dicotyledons during a time interval (Cretaceous-Early Tertiary) that is famous for marking the extinction of the dinosaurs and the rise of mammals, but is also significant in the development of modern vegetation and the diversification of flowering plants.

BIG BEND NATIONAL PARK

Big Bend National Park provides a unique setting for studying changes in wood structure through time. In Big Bend there are localities with petrified trees ranging in age from Cretaceous through Miocene (Busbey and Lehman, 1989; Koepp, Sanchez, Stephens, and Stephens, personal communications). A series of publications documenting the types of fossil woods and their ecologic and systematic significance has been initiated (Wheeler, 1991; Wheeler, Lehman, and Gasson, in press; Wheeler and Lehman, ms. in preparation). Most studies of fossil woods are based on fragments whose position within the plant is not known. Often fragments are small and it is not always possible to tell whether they represent root or stem wood. Most of our knowledge of wood structure (both systematic and ecologic) is of mature stem wood and so it can be difficult to determine affinities or make ecologic inferences for small samples that might represent root or branch wood. The fossil logs of Big Bend provide an opportunity to control sampling, in other words, a collector can be sure of where the sample came from, and a minimum diameter of the tree directly measures and with that information the height of the tree estimated.

What is particularly important about the localities within Big Bend is that there is considerable information on the geology and vertebrate paleontology in the Park (e.g. Lehman, 19985,1987,1990; Rowe,et al.1992). Thus, its possible to put the paleobotanical work into a stratigraphic framework, and interpretations of the woody plants' ecological anatomy can be integrated with the information derived from other studies.

How Big and How Common were Hardwoods During the Cretaceous? Woods from the Late Cretaceous (Campanian and Maastrichtian) of Big Bend National Park.

Although angiosperms were diverse and dominate late Cretaceous palynofloras and compression floras (Crane, 1990; Upchurch and Wolfe, 1987), it has been suggested that dicotyledonous trees were restricted to riverbanks and disturbed habitats and did not form forests (Wing et al., 1993). Moreover, it has been generalized that "Late Cretaceous angiosperm tree trunks were mainly less than 10 cm in diameter and thus were of a size that they could have easily been knocked over by ceratopsids" (Dodson, 1993: p. 230). The preceding statement is based primarily on studies of fossils from the northern Rocky Mountains. There was latitudinal variation in the vertebrate faunas (Lehman, 1987), and so it should not be surprising that there is comparable variation in vegetation. The fossil woods from Big Bend National Park, Texas, suggest that some generalizations about Late Cretaceous angiosperms need revision because dicotyledons more than 10 cm in diameter were common in the Late Cretaceous of the Big Bend region.

Throughout the Aguja Formation (Campanian, Late Cretaceous) of Big Bend National Park, Texas, there occur petrified woods. At some localities dicotyledonous logs with a diameter of more than 50 cm are common, while at other localities, there are only relatively small wood fragments (2-3 cm diameter). Some localities and depositional settings have only dicotyledons, others have conifers and palms. To date, it appears that dicotyledons are the most common woods in the Aguja Formation, although only six types of dicotyledonous woods, all species different from present-day trees (Rich et al., 1986) suggest the fossil trees with a 50 cm diameter would have been more than 30 meters tall. These data indicate that Cretaceous angiosperms were as large as some of the common hardwoods of North America (e.g., sycamore, *Platanus occidentalis*).

In the younger Javelina Formation (Maastichtian, Late Cretaceous), there occurs *Javelinoxylon*, an ancient representative of the primarily tropical plant group Malvales. *Javelinoxylon* was a tree that had a diameter in excess of 70 cm, and so also was taller than 30 m (>100 feet) (Wheeler, Lehman, Gasson, in press). Additionally, there are stump fields in the lower portion of the Javelina with the stumps seemingly in growth position. Some of these stumps are over 1 m in diameter, and have exposed roots over 3 m long. Work on these woods is just beginning, but such occurrences can provide information about the spacing of dicotyledonous trees in the Cretaceous landscape, as well as the range in sizes within different types of Cretaceous trees. Some of these trees are of interest because they show evidence of heartrot; some stumps had hollow centers that were infilled with sediment during the Cretaceous. They can provide data about the interactions between trees and decay organisms of the past.

What Tree Types Survived the Terminal Cretaceous Event? North America's Best Known Paleocene

Dicotyledonous Woods, Big Bend National Park

For the whole world fewer than 20 types of fossil dicotyledonous woods of unequivocal Paleocene age have been described. The only Paleocene dicotyledonous woods described from North America are from the Black Peaks Formation of Big Bend (Wheeler, 1991). In the Tornillo Flats region of the park, there are many logs, but the vast majority of these logs are of a single type, a wood assigned to the genus *Paraphyllanthoxylon. Paraphyllanthoxylon* type wood is seen in at least four different extant plant families, all of which are primarily tropical (Euphorbiaceae, Lauraceae, Anacardiaceae, Burseraceae). Moreover, all of these woods lack distinct growth rings as is characteristic of U.S. woods at present. The lack of distinct growth rings and the size and number of vessels (water conducting elements) suggest that the woods grew in tropical climates, with year-round abundant water and warm temperatures, an environment that is in marked distinction to the Big Bend region of the present-day. In Big Bend, another Paleocene locality with abundant and large logs has been found, and superficial examination of these woods suggests that they too belong to the genus *Paraphyllanthoxylon.*

Woods with the structural patterns of Paraphyllanthoxylon are among the earliest known hardwoods, occurring in the Albian (mid-Cretaceous). Such woods were widespread in the Cretaceous and have been recovered from the Cretaceous of California, Alabama, Arizona, New Mexico, southern Illinois, Maryland, Utah, Baja California, Europe, and South Africa. This structural pattern is of interest as it was common in the Cretaceous as well as the Paleocene. Because it is rare to find attachment between reproductive structures (which are most important in defining plant families) and vegetative structures (woody stems or twigs) there is no way of being sure how many species of plants this one wood represents. It is likely that this successful wood pattern occurred in more than one species or genus. Additional work searching for woods of Paleocene age is important for shedding light on which tree types were successful in both the Cretaceous and Paleocene and were able to survive the Cretaceous-Tertiary terminal event, which was marked by massive extinctions.

YELLOWSTONE NATIONAL PARK

When Did Present-Day Genera Appear, and Tropical Forests? Yellowstone National Park - Eocene Forests - Mixtures of extinct and extant genera.

The Early Middle Eocene "Fossil Forests" of Yellowstone National Park are one of the most spectacular localities for early Tertiary fossil plants. At Specimen Ridge, Amethyst Mountain, and the Gallatin Forests there are "layer cakes" of fossil forests that were entombed in successive volcanic eruptions (Smedes and Prostka, 1972). Many of the fossil stumps are upright. There is debate about whether these stumps represent in situ remains of the fossil forests or whether some or all stumps were transported (Fritz, 1980; Yuretich, 1984; Wing, 1987). Resolution of this question is important for paleoecological inferences, but pending its resolution, the well-preserved woods at Yellowstone provide data that are useful in reconstructing the histories of different plant families and changes in dicotyledonous wood structure during the Tertiary.

The Middle Eocene was one of the warmest intervals of recent geologic history. The evolutionary radiations of many extant woody dicotyledonous families are recorded in the Eocene, e.g., in the Birch Family (Betulaceae; Crane, 1989), Beech/Oak Family (Fagaceae; Crepet and Nixon, 1989), Walnut Family (Juglandaceae; Manchester, 1989a), and Elm Family (Ulmaceae; Manchester, 1989b).

Although many of the stumps at Yellowstone are conifers, there are many dicotyledonous leaves. Conifer wood may be more likely to be preserved, as conifer ligins (the complex chemicals that make woody cell walls rigid) may be more resistant to decay organisms than hardwood ligins. Also, conifers may be more permeable as there numerous interconnections between all the cells in conifer woods, so that petrification via infiltration of the cell wall with silica-carrying water is more likely in conifers than in angiosperms.

Among the hardwoods (dicotyledonous angiosperms) recognized at Yellowstone, some have wood structure identical to modern plants and at present occur in warm temperate to subtropical regions (e.g., cherry - *Prunus*, family Rosaceae; alder - *Alnus*, family Betulaceae; ironwood - *Carpinus*, family Betulaceae), others resemble trees that today occur primarily in the tropics (woods of the Sterculiaceae, Magnoliaceae, Lauraceae) (Wheeler et al., 1977, 1978). Some differ from extant plants. The sycamore-like woods of Yellowstone have a combination of features that indicates they are related to modern sycamores (*Platanus*), but differ in some features that wood anatomists have long considered to be "primitive" features. In these Eocene sycamore-like woods all the end walls of the water conducting cells (vessel elements) have bars across them (scalariform perforation plates), while modern sycamores, even those growing in Viet-Nam, have some water conducting with end walls without bars across them, and large open ends (simple perforation plates). The wood that resembles Chinese elm (*Zelkova)* differs from the modern genus in its distribution of vessel diameters.

FLORISSANT NATIONAL MONUMENT

<u>Is the Late Eocene climatic change recorded in dicotyledonous woods?</u>

There is a wide body of evidence from marine and terrestrial sediments that indicate that the end of the Eocene was marked by a dramatic change in climate (Wolfe, 1978). The characteristics of the three dicotyledonous wood types recovered from Florissant National Monument reflect this dramatic change.

One of the primary functions of wood is water conduction; the structure of wood reflects water availability. Carlquist (1977, 1988) and Baas (1986; Baas et al., 1983) have studied the geographic and ecologic distribution of different anatomies and have shown that there exists ecological trends in dicotyledonous wood anatomy. Their work indicates that with increasing drought or decreasing temperature there is an increase in vessel frequency, percentage of vessel groupings, incidence of spiral thickenings in the vessel elements, a shortening of vessel elements, and a decrease in vessel diameter. Ring porous dicotyledonous woods are characterized by the vessels of the first-formed portion of a growth ring being markedly larger than the vessels in the later-formed portion of a growth ring. In the present-day flora, ring porous woods are common in north temperate region, but very rare in the tropics and absent from very high latitudes.

Two of the three wood types from Florissant are ring porous with relatively short vessel elements, and one has spiral thickenings in the vessel elements. The diffuse porous wood (diffuse porous woods have vessels of near equal size throughout a growth ring) has many vessel groupings, and the average vessel diameter is less than 100 micrometers, a diameter usually categorized as small. All three types have distinct growth rings. Thus, the anatomies of these woods indicate a markedly seasonal climate.

CONCLUSION

The localities briefly discussed above illustrate the uses that fossil dicotyledonous woods have for answering questions about the past distribution and diversity of ancient angiosperms. The differences between the Cretaceous and Paleocene woods from Big Bend, the Middle Eocene woods from Yellowstone, and the Late Eocene woods from Florissant illustrate the dramatic changes in climate and vegetation type that have been documented for the Cretaceous through early Tertiary (Wolfe, 1978; Wing, 1987; Upchurch and Wolfe, 1987). The Cretaceous and Paleocene woods of Big Bend lack distinct growth rings and are generalized in their structure, the Middle Eocene woods of Yellowstone have growth rings and most are referable to extant families and genera, the Late Eocene woods of Florissant have distinct growth rings and suggest pronounced seasonality and also have anatomy like that of extant woods. Continuing work on woods from these three areas will refine our knowledge of the history of woody plants, and wood itself, an important tissue deserving of study, as it functions in water conduction, support, and storage for trees and shrubs.

REFERENCES

Baas, P., 1986. Ecological patterns of xylem anatomy; in Givnish, T.D., ed., On the economy of plant form and function: Cambridge, Cambridge University Press, p. 327- 352.

Baas, P., Werker, E. and Fahn, A., 1983. Some ecological trends in vessel characters: International Association of Wood Anatomists Bulletin, v. 4, p. 141-159.

Busbey, A.B. and Lehman, T.M., 1989. Vertebrate paleontology, biostratigraphy and depositional environments, latest Cretaceous and Tertiary, Big Bend area, Texas: Guidebook, Field Trip Numbers 1A, B, and C. 49th Annual Meeting of the Society of Vertebrate Paleontology, Austin, Texas.

Carlquist, S., 1988. Comparative wood anatomy: New York, Springer-Verlag.

Carlquist, S., 1975. Ecological strategies of xylem evolution: Berkeley, University of California Press.

Crane, P.R., 1989. Early fossil history and evolution of the Betulaceae; in Crane, P.R. and Blackmore, S., eds., Evolution, systematics, and fossil history of the Hamamelidae, v. 2: 'Higher' Hemamelidae, Systematics Association Special Volume no. 40B, Charendon Press, p. 87- 116.

Crepet, W.L. and Nixon, K.C., 1989. Earliest megafossil evidence of Fagaceae: phylogenetic and biogeographic implications: American Journal of Botany, v. 76, p. 842-855.

Dodson, P., 1993. Comparative craniology of the Ceratopsia: American Journal of Science, v. 293, p. 200-234.

Fritz, W.J., 1980. Reinterpretation of the depositional environments of the Yellowstone "fossil forests": Geology, v. 8, 309-313.

LaPasha, C.A. and Wheeler, E.A., 1987. A microcomputer based system for computer-aided wood identification: International Association of Wood Anatomists Bulletin, v. 8, p. 347-354.

Lehman, T.M., 1990. Paleosols and the Cretaceous/Tertiary transition in the Big Bend region of Texas: Geology, v. 18, p. 362-364.

Lehman, T.M., 1987. Late Maastrichtian paleoenvironments and dinosaur biogeography in the western interior of North America: Paleogeography, Paleoclimatology, Paleoecology, v. 6, p. 189-217.

Lehman, T.M., 1985. Sedimentology, stratigraphy, and paleontology of Upper Cretaceous (Campanian-Maastrichtian) sedimentary rocks in Trans Pecos Texas [Ph.D. Dissertation]: Austin, University of Texas, 199 p.

Manchester, S.R., in press. Fruits and seeds of the middle Eocene Nut Beds flora, Clarno Formation North-central Oregon: Paleontographica Americana.

Manchester, S.R., 1989a. Early history of the Juglandaceae: Plant Systematics and Evolution, v. 162, 231-350.

Manchester, S.R., 1989b. Systematics and fossil history of the Ulmaceae; in Crane, P.R. and Blackmore, S., eds., Evolution, Systematics, and fossil history of the Hamamelidae, v. 2, 'Higher' Hamamelidae, Systematics Association Special Volume no. 40B, Oxford, Clarendon Press, p. 221-252.

Rich, P.M., Helenurm, K., Kearns, D., Morse, S.R., and Palmer, M.W., 1986. Height and stem diameter relationships for dicotyledonous trees and arborescent palms of Costa Rican tropical wet forest: Bulletin of the Torrey Botanical Club, v. 113, p. 241-246.

Rowe, T.R., Cifelli, R.L., Lehman, T.M., and Weil, A., 1992. The Campanian Terlingua local fauna, with a summary of other vertebrates from the Aguja Formation, Trans-Pecos Texas: Journal of Vertebrate Paleontology, v. 12(4), p. 472-493.

Smedes, H.W. and Prostka, H.J., 1972. Stratigraphic framework of the Absaroka volcanic supergroup in the Yellowstone National Park region: U. S. Geological Survey, Professional Paper 729-C, p. 1-33.

Upchurch, G.R., and Wolfe, J.A., 1987. Mid-Cretaceous to Early Tertiary vegetation and climate: evidence from fossil leaves and woods; in Friis, E.M., Chaloner, W., and Crane, P., eds., The origins of angiosperms and their biological consequences: Cambridge, Cambridge University Press, p. 75-105.

Wheeler, E.A., 1991. Paleocene dicotyledonous trees from Big Bend National Park, Texas: Variability in wood types common in the Late Cretaceous and Early Tertiary, and ecological inferences: American Journal of Botany, v. 78, p. 658-671.

Wheeler, E.A. and Baas, P., 1991. A survey of the fossil record for dicotyledonous woods and its significance for evolutionary and ecological wood anatomy: International Association of Wood Anatomists Bulletin, v. 12, p. 271-332.

Wheeler, E.A., Lehman, T.M., and Gasson, P., in press. *Javelinoxylon*, a new genus of malvalean tree from the Upper Cretaceous of Big Bend National Park, Texas: American Journal of Botany.

Wheeler, E.A., Pearson, R.G., LaPasha, C.A., Zack, T., and Hatley, W., 1986. Computer-aided wood identification. Reference Manual: North Carolina Agricultural Research Service Bulletin 474, 160 p.

Wheeler, E.F., Scott, R.A., and Barghoon, E.S., 1978. Fossil dicotyledonous woods from Yellowstone National Park, II: Journal of the Arnold Arboretum (Harvard), v. 29, p. 1-26.

Wheeler, E.F., Scott, R.A., and Barghoon, E.S., 1977. Fossil dicotyledonous woods from Yellowstone National Park, I: Journal of the Arnold Arboretum (Harvard), v. 58, p. 280-306.

Wing, S.L., 1987. Eocene and Oligocene floras and vegetation of the Rocky Mountains: Annals of the Missouri Botanical Garden, v. 74, p. 748-784.

Wing, S.L., Hickey, L.J., and Swisher, C.C., 1993. Implications of an exceptional fossil flora for Late Cretaceous vegetation: Nature, v. 363, p. 342-344.

Wolfe, J.A., 1978. A paleobotanical interpretation of Tertiary climates in the northern hemisphere: American Scientist, v. 66, p. 694-703.

Yuretich, R.F., 1984. Yellowstone fossil forests: new evidence for burial in place: Geology, v. 12, p. 159-162.

Back to Table of Contents